A.J. Gaston
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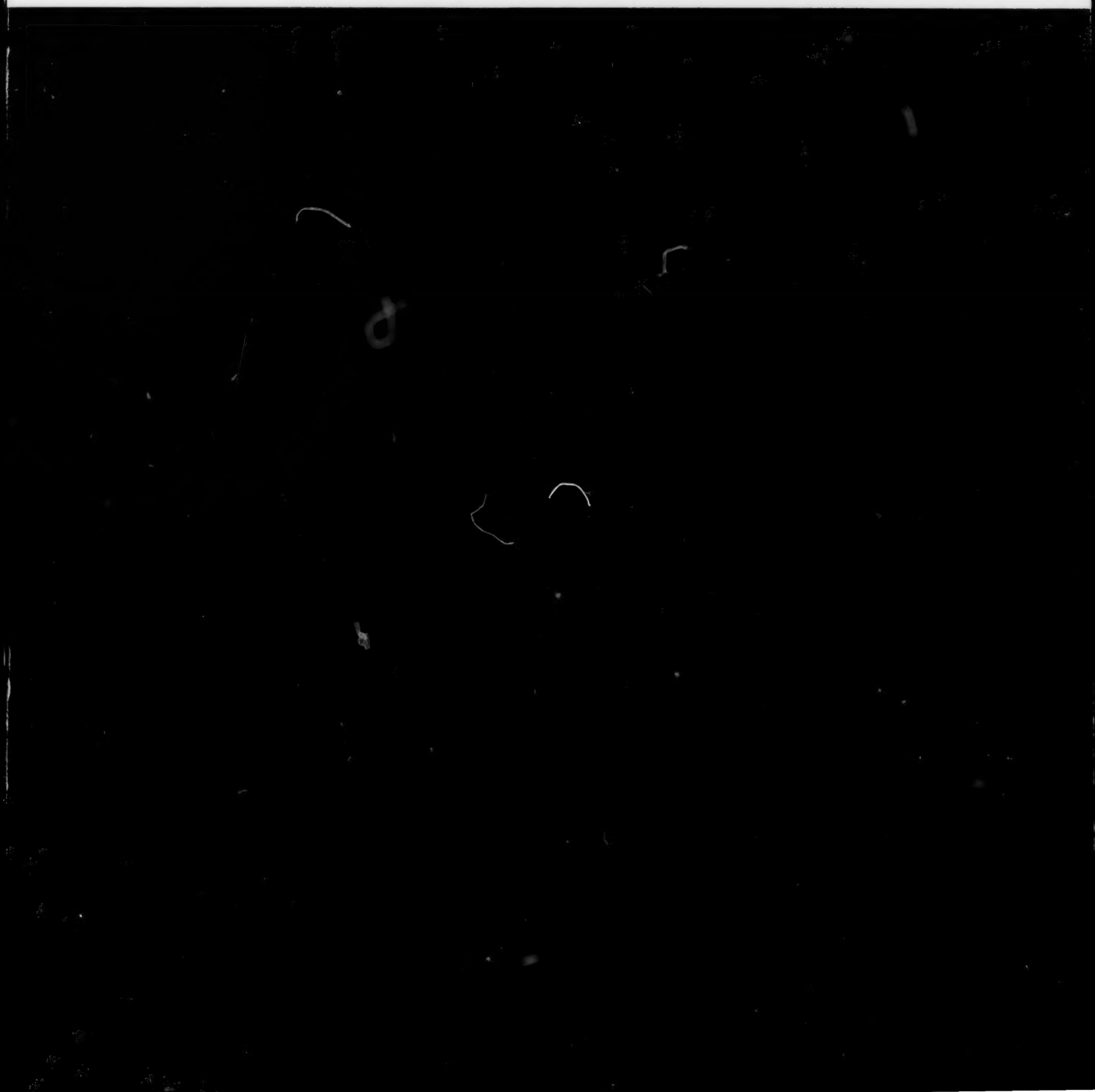
The interpretation of aerial surveys for seabirds: some effects of behaviour



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The interpretation of aerial surveys for seabirds: some effects of behaviour

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Abstract

Aerial surveys have been used extensively to observe the distribution and abundance of marine birds at sea. Although biases caused by weather and sea conditions, aircraft type, and the state and experience of the observer have been discussed by others, little has been done to interpret the effect of biological variables inherent in the behaviour of the birds.

In this paper we explore five ways in which the analysis of aerial survey data can enhance our understanding of seabird distributions compared with inspection of the raw data alone. We consider the effects of (1) colony attendance, (2) travel time between colony and feeding grounds, (3) relative motion of birds and aircraft, and (4) duration and frequency of dives. We also consider the effect of flock size on the accuracy of survey results and the adequacy of sampling.

We give examples that illustrate the degree to which the proposed corrections may improve the interpretation of results.

Introduction

Aerial surveys have been used extensively to document the offshore distribution of seabirds and marine mammals in eastern Canadian waters. These surveys attempt to identify the relative importance of different areas for seabirds, on the assumption that this knowledge may be useful in planning and implementing offshore exploration, extraction, and marine transport of oil.

In evaluating aerial survey results for use in environmental impact assessments, priority is necessarily given to areas where birds are observed feeding or are for any reason in contact with the sea surface. The same is true if the biological significance of observed distributions is to be discussed. In some cases, therefore, it is necessary to separate records of birds that are flying from those on the sea, and we shall concentrate on the interpretation of the latter.

The possible biases and inaccuracies of aerial surveys have been extensively discussed (Johnson *et al.*, unpubl.; MacLaren, unpubl.; Nettleship and Gaston 1978; McLaren 1982; Savard 1982; Orr and Ward 1982; Harrison 1982), although quantitative data on their magnitude is not available. Consequently, most discussion has been qualitative. Problems perceived fall into four categories:

(1) Effects of weather, light, and sea conditions on the detectability of seabirds;

(2) The relative detectability of different seabird species, in relation to size, plumage, behaviour, and degree of aggregation;

(3) Observer effects, including seating position, experience, and fatigue;

(4) Effects of aircraft characteristics on observers' field of vision and the effects of speed and altitude on the observers' ability to detect seabirds.

All of the above factors influence the likelihood that birds will be detected and accurately enumerated. However, even if counts of birds were made with 100% accuracy, or the degree of bias estimated with great precision, the interpretation of differences in the number of birds seen in different areas or at different times would vary as a result of the birds' behaviour. This statement is particularly true during the breeding season. Some of these effects can be predicted on the basis of behavioural studies either at breeding colonies or at sea, and we shall attempt to explore some of these problems and estimate their approximate magnitude.

We deal with sources of bias and inaccuracy under five headings (Table 1). Some of these sources can be estimated and corrected for in specific situations (1, 2, 3), some may be susceptible to estimation with additional research (4), and others may be minimized through the initial design of surveys (1, 5). Correction factors derived for certain sources of bias are applicable to ship-board observations as well as aerial surveys.

Table 1
Sources of bias and inaccuracy in aerial surveys for seabirds resulting from the behaviour of the birds

Source of bias and inaccuracy	Species affected	Season
1. Colony attendance	All seabirds	Breeding season from 1–2 months prior to laying
2. Travel times between colonies and feeding grounds	Long distance foragers; fulmars, petrels, Gannets, kittiwakes, auks	Breeding season from 1–2 months prior to laying
3. Relative motion of birds and aircraft	All seabirds, but particularly fast fliers; auks, shearwaters	Breeding season and periods of migration
4. Duration and frequency of dives	Underwater swimmers; cormorants, auks, shearwaters	All seasons
5. Degree of aggregation	Flock feeders; fulmars, shearwaters, gulls, kittiwakes	Variable

Methods

1. Colony attendance

Aerial surveys normally avoid the immediate vicinity of large seabird colonies to minimize disturbance. Consequently, birds attending the colony are outside the sampling pools of most aerial surveys. Numbers observed at sea are therefore inversely related to numbers present at the colony. Gaston and Nettleship (1981) demonstrated this inverse relationship in a study on Thick-billed Murres *Uria lomvia* from the colony at Prince Leopold Island.

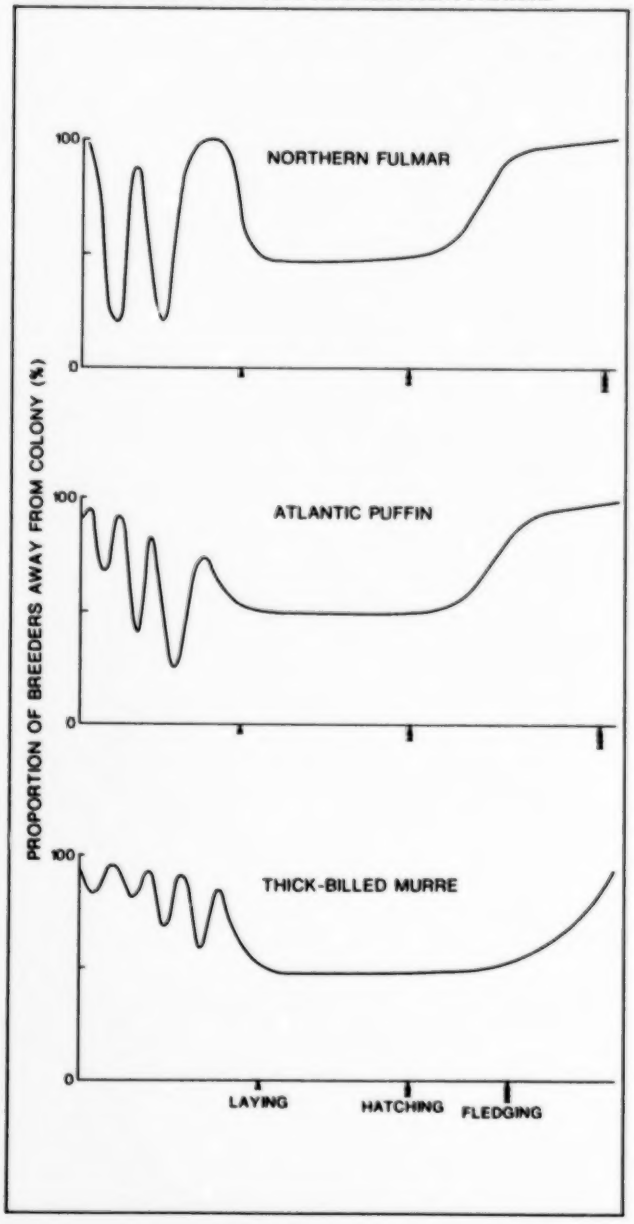
For most seabirds, at least half of the population is present at the colony at any one time from the median date of laying to at least the median date of hatching, in some cases longer. The number of birds present at the colony before laying fluctuates widely, sometimes in a cyclical fashion (Northern Fulmar *Fulmarus glacialis*, Greene and Nettleship unpubl.; Atlantic Puffin *Fratercula arctica*, Nettleship 1972; Razorbill *Alca torda*, Lloyd 1975; Common Murre *Uria aalge*, Birkhead 1978), sometimes irregularly, in response to weather conditions (Common Murre [one year], Birkhead 1978; Thick-billed Murre, Gaston and Nettleship 1981).

Diurnal patterns of attendance may also influence the number of birds away from the colony. These patterns may follow a solar cycle, as in most murre populations (Birkhead 1978; Gaston and Nettleship 1981), or a tidal cycle, as in at least one population of Common Murres (Slater 1976).

The magnitude of the effects of colony attendance on numbers recorded at sea can be estimated by comparing the proportion of the population present at the colony for different species and stages of the breeding cycle. In most auks and the Northern Fulmar, numbers attending during the pre-laying period fluctuate between nil and more than half the breeding population so that maximum numbers at sea are at least twice the minimum. During the incubation period, virtually all seabirds incubate their eggs continuously so that a minimum of half the population is present at the colony throughout. Attendance during the chick-rearing period generally declines as the chicks get older, except for the murres and the Gannet *Sula bassana*, where one parent remains with the chick until it leaves the nest site. We have summarized seasonal changes in the proportion of the population away from the colony in Figure 1.

The interpretation of aerial survey results for species that show synchronized periods of attendance at their breeding colonies during the pre-laying period is very difficult, unless simultaneous observations can be made at the colony. Since such observations are not usually possible in practice, surveys made during the pre-laying period must be interpreted with caution.

Figure 1
Approximate proportion of the breeding population at sea at different stages of the breeding cycle, for three species: Northern Fulmar *Fulmarus glacialis*, Atlantic Puffin *Fratercula arctica*, and Thick-billed Murre *Uria lomvia*



Johnson *et al.* (unpubl.) have presented data that give some indication of how attendance patterns may affect the interpretation of survey results. During weekly surveys in eastern Lancaster Sound, they recorded approximately 20 000 Northern Fulmars on transects flown during late June and early July 1976. Subsequent surveys, in the first half of August, revealed 27 000–40 000 Northern Fulmars. If we had concluded that the importance of eastern Lancaster Sound as a feeding area had increased over this period we should probably have been wrong. We know that in 1976 fulmars hatched about the end of July in the Lancaster Sound area (Nettleship 1977). Hence, the increase in numbers observed at sea was almost exactly what we would have expected, once parents had ceased to brood their chicks and had begun to spend most of their time away from the colony. We may conclude, therefore, that the number of Northern Fulmars finding their food in eastern Lancaster Sound remained stable over the period concerned.

Diurnal changes in the number of birds attending their breeding colonies may be considerable and the extent of such variation changes with the breeding cycle. Ideally, surveys should be replicated and randomized with respect to time of day or flown when most birds are known to be at sea, but in practice this is likely to be prohibitively expensive. For the Black Guillemot *Cepphus grylle*, a species whose attendance may fluctuate from nil to practically 100% over 24 h (Petersen 1981; AJG, pers. obs.), it is probably important to compare only surveys made at similar times of day, or, where comparisons are made between areas of different latitude, at similar light intensities. Actually, most surveys are normally flown in the middle of the day when the majority of Black Guillemots are away from their colonies, because guillemots are only one of a number of species being recorded. Consequently, most aerial surveys take place when the majority of guillemots are away from their colonies.

2. Travel time between colony and feeding grounds

During the breeding season, particularly during incubation and chick rearing, seabirds must commute regularly between their colony and their feeding areas. Foraging ranges, flight speeds, and frequency of visits to the colony determine the amount of time spent in the air, and consequently limit the amount of time spent feeding. For a given species the time spent travelling is directly proportional to the foraging range. If we assume that all breeding birds feeding within the limits of the colony's foraging range are equally successful in supplying their chicks with food, then it follows that birds feeding close to the colony must devote a longer period of time to feeding than those feeding further away, for which travel time comprises a greater portion of their overall time budget. Counts made a long way from the colony will therefore underestimate the number of birds using the area for feeding because many birds that use the area will be in transit at the moment of the survey. Besides, counts that include birds in flight will tend to exaggerate the importance of areas close to the colony, where many birds are in transit to more distant feeding areas.

When recording seabirds that feed either by plunge diving, such as Gannets, terns *Sterna* sp., and, in some cases, shearwaters *Puffinus* spp., or by picking food from the surface without landing, such as petrels *Oceanodroma* spp., it is difficult to distinguish birds that are feeding from those travelling to and from their feeding grounds. When recording species that alight on the water before feeding, it is useful to keep separate records for birds seen flying to allow a better assessment of the relative importance of different areas for feeding.

A general equation for time spent travelling between breeding sites and feeding areas is given by:

$$T_a = 2VL/s \qquad [1]$$

where T_a = flying time ($h \cdot day^{-1}$); V = number of daily visits to the colony by each parent; L = distance from colony to feeding ground (km); s = flight speed ($km \cdot h^{-1}$).

The amount of bias introduced by time spent travelling can be estimated in two cases; (*a*) when birds in the water and in the air are recorded separately, (*b*) when no distinction is made.

(*a*) To correct observed numbers seen feeding (N_o) so that they represent the total number of birds using an area over a day, we need to add the birds in flight at a given moment (N_a), and the birds remaining at the colony that have used or will use the area (N_b). For species where the members of a pair share incubation duties equally, the proportion of breeders in the air at any one time is the same as the fraction of a day each individual spends flying

$$N_a/(N_a + N_o + N_b) = VL/12s = \frac{T_a}{24} \qquad [2]$$

If we assume that time spent away from the colony is devoted exclusively to travelling (T_a) and feeding (T_o), then the amount of time spent feeding on average will be:

$$T_o = 24 - T_b - T_a = 24 - T_b - \frac{2VL}{s} \qquad [3]$$

From this we can obtain a general formula to determine the number of birds using a given area over 24 h (N_f):

$$N_f = N_o/[1 - \frac{T_b}{24} - \frac{VL}{12s}] \qquad [4]$$

In the simplest case, where birds exchange incubation and brooding duty rapidly, and the off-duty partner leaves immediately, this formula reduces to:

$$N_f = 2N_o/[1 - \frac{VL}{6s}] \qquad [5]$$

In either case, if T_b is known from observations at the colony concerned or for the species in general, we can obtain an estimate of N_f.

Figure 2 shows the relationship of observed numbers (N_o) to total numbers using an area (N_f). As illustrated, the amount of bias introduced increases in proportion to the time spent travelling (T_a). Consequently, this correction is relatively insignificant at distances up to 40 km from the colony, but becomes very significant beyond 100 km. An example of a foraging distribution corrected in this way is shown in Figure 3, based on observations made around the large Thick-billed Murre colonies at Digges Sound.

(*b*) If survey counts make no distinction between flying birds and those on the water, or if the birds recorded do most foraging in flight, counts in areas close to the colony will be biased by the inclusion of birds flying to and from areas further away. If birds in transit are not being con-

Figure 2
Amount of time spent flying (T_a) and ratio of birds actually using a particular area to those present at a given moment (N_f/N_a), in relation to distance from the colony (based on equation [3], using $V = 2$, $s = 60$ km·h^{-1}) (T_a, solid line; N_f/N_a, broken line)

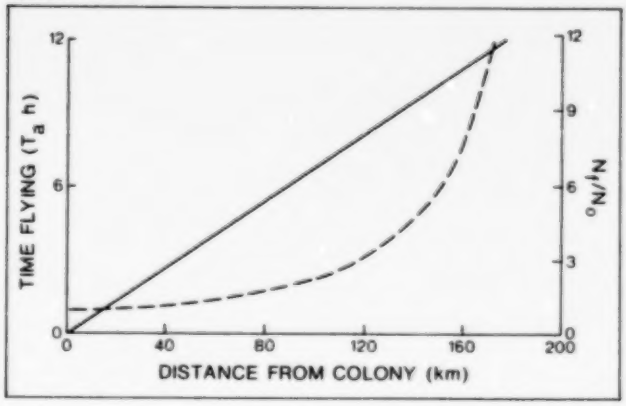


Figure 3
Correction shown in equation [3] applied to aerial survey data on Thick-billed Murres *Uria lomvia* around Digges Sound, NE Hudson Bay, on 9 August 1981 ($V = 1$, $s = 58$ km·h^{-1}). Original observations, broken line; corrected figures, solid line

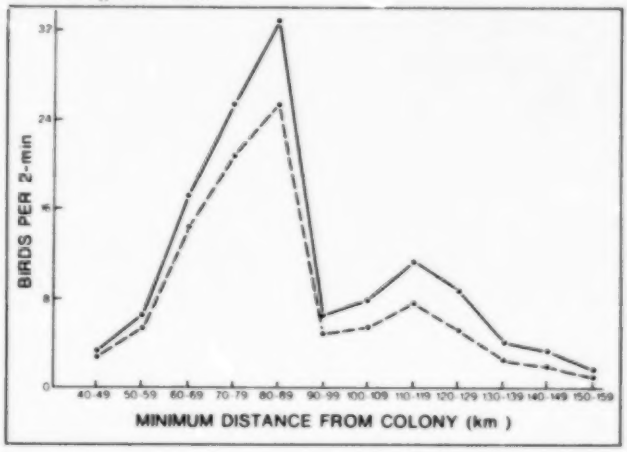
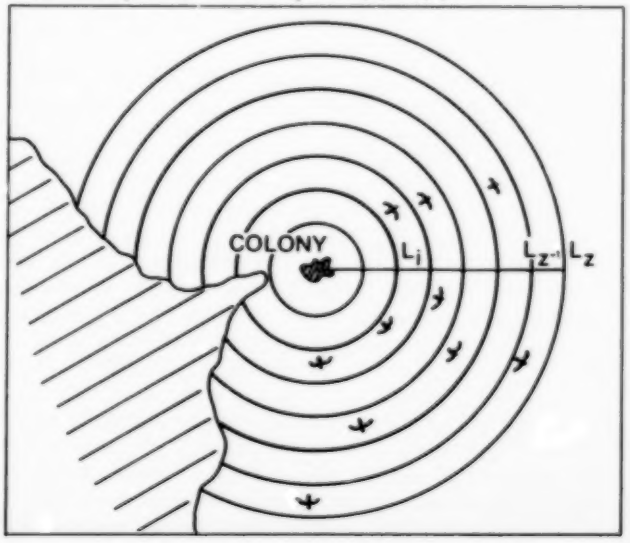


Figure 4
Illustration of parameters used in equations [6] and [7]



centrated by following shorelines, observed densities of birds, at different distances from their colony, can be corrected to yield an estimate of the actual proportion of the population feeding at different distances.

This correction is made by dividing the area surrounding the colony into concentric zones (Fig. 4) and by using the number of birds seen in the outermost zone as an estimate of the actual numbers feeding in that zone at the time of the survey. The proportion of the colony feeding in each zone can then be estimated, working inwards from the outermost zone, by calculating the number of birds travelling through each zone which are going to and from zones further away. As in the preceding example, the method requires a knowledge of the flight speed, of the number of daily visits to the colony, and of the time each breeding adult spends foraging each day.

To calculate the total number of birds using the outermost zone (z) for foraging, we use a modification of equation [4]:

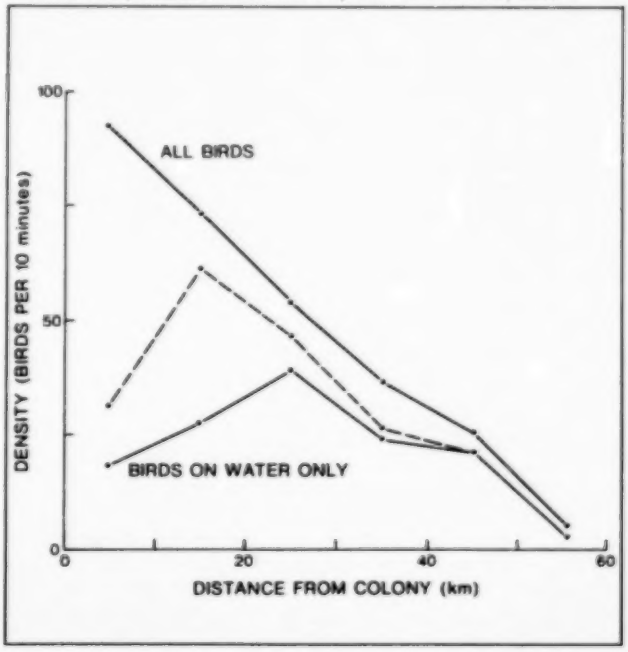
$$N_{fz} = \frac{24 n_{oz}}{24 - T_b - (2VL_{z-1})/s} \qquad [6]$$

where N_{fz} and n_{oz} are, respectively, the total number, and the observed number of birds feeding in the outermost zone.

Working inwards from the outermost zone, we then calculate numbers feeding in each successive zone (N_{fi}):

$$N_{fi} = \frac{24 s\, n_{oi} - [2V(L_i - L_{i-1}) \sum_{j=i+1}^{z} N_{fj}]}{(24 - T_b)s - 2VL_{i-1}} \qquad [7]$$

Figure 5
Example of the correction given in equations [6] and [7], based on data for Thick-billed Murres *Uria lomvia*, off Hantzsch Island, SE Baffin Island (from MacLaren Marex, unpubl.). The dashed line represents the estimate of the proportion of birds feeding, based on the upper solid line giving all sightings. The lower solid line shows the actual counts of birds on the water, hence presumably feeding. The outermost feeding zone was taken to be 40–50 km from the colony because numbers seen beyond 50 km were very small



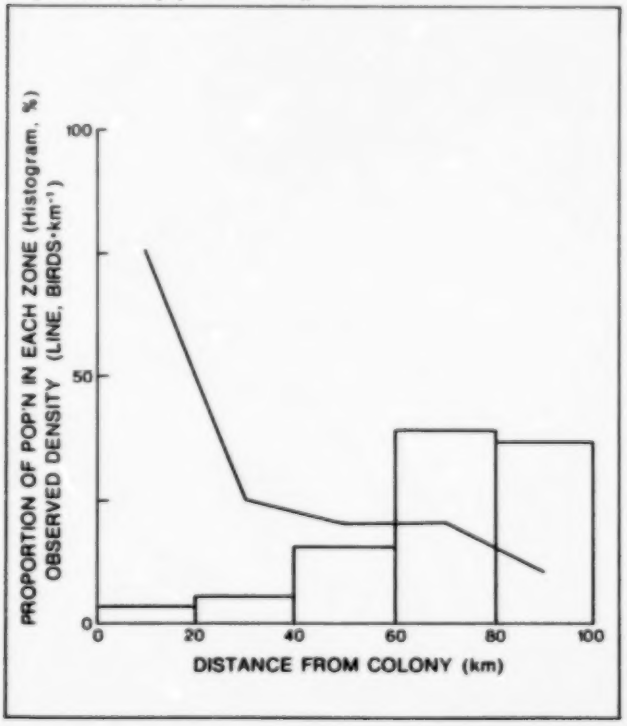
where i = innermost zone
$z-1$ = next to outermost zone
z = outermost zone
j = $i+1$ = next to innermost zone

and where n_{ij} is the average number of birds seen feeding in or flying over the innermost zone (i). We have given the derivation of this formula in Appendix 1. (Note that for the next to outermost zone ($z-1$), $\Sigma N_{ij} = N_{iz}$.)

In Figure 5, we illustrate the use of this technique, based on figures from a boat survey around the Thick-billed Murre colony at Hantzsch Island (MacLaren, unpubl.). The dashed line shows the estimated "true" density of feeding birds, based on the densities of all birds seen (the upper solid line). The lower solid line shows the densities of birds observed on the water only, presumably those actually feeding. The estimated (dashed) line clearly gives a better fit to the real situation than figures based on all sightings.

Like other corrections for travel time, this correction increases in importance with foraging range. Figure 6 shows a hypothetical example, based on figures appropriate for Thick-billed Murres: a maximum foraging range of 100 km, a flight speed of 58 km·h^{-1}, and two trips to the colony each day. This example demonstrates the dramatic difference between observed densities and the actual proportion of birds feeding at different distances from the colony. This type of correction is particularly important for species such as petrels, fulmars, and Gannets that search for their prey in flight, spending little time in or on the water.

Figure 6
Example of a correction based on Appendix 1 for a 100-km foraging radius. The solid line gives observed densities; the histogram shows the calculated proportions of the population feeding in each zone



3. Relative motion of birds and aircraft

Flying birds encountered on aerial surveys sometimes follow a uniform heading, as in cases where they are commuting between a colony and a limited feeding area, or where they are on migration. To obtain an estimate of the actual rate of passage, observed rates of movement must be corrected for the relative speed of birds and aircraft.

In most aerial surveys the aircraft is travelling faster than the birds by a factor of 2–4 times. If the aircraft were travelling much faster than the birds (>10 times as fast), then the latter would be effectively stationary relative to the observer. Alternatively, an observation platform travelling much more slowly than the birds (a slow-moving boat) would be effectively stationary relative to the birds. A correction for relative speed is most desirable where the speed of birds and the speed of the observer do not differ by more than a factor of 5.

For this correction, we consider a square kilometre of ocean over which birds are passing with a uniform heading. If the birds fly at an average speed of s km·h^{-1}, and the density of birds at a given instant is D birds·km^{-2}, we can estimate the rate of passage (e birds·km^{-1}·h^{-1}).

Each bird spends s^{-1} h in the block. Hence, to maintain D birds in the block, D birds must enter every s^{-1} h. Therefore:

$$e = D/s^{-1} = Ds \qquad [8]$$

If s is a known constant for the species concerned, we can find e by estimating D. Given these conditions, a correction for relative speed is required.

We now consider the situation in Figure 7, where bird and aircraft headings make an angle $\theta°$. If $\theta° < 90°$, the number of birds counted over a given distance and within a fixed transect width will be less than the number actually present in the area covered at a given instant. The explanation is that the component of their heading that takes them in the same direction as the aircraft means that some birds will leave the transect before they have been counted. Alternatively, if $\theta° > 90°$, the reverse will be true, and the number of birds counted will exceed the actual number present at any instant. If the observer counts birds within an area stretching some distance ahead of the aircraft, a further correction will be necessary to include birds that enter the field of view during the time it takes to move from the initial position (A, Fig. 7) to the limit of forward vision (B).

The actual rate of movement of flying birds can be calculated from observed rates of movement using the equation [9] (also see App. 2, equation [3]):

$$e = \frac{Ns}{t[(S - s\cos\theta)W + as\sin\theta]} \qquad [9]$$

where s = speed of birds (km·h^{-1})
S = speed of aircraft (km·h^{-1})
W = transect width (km)
a = distance observer can see ahead (km)
N = total birds counted
t = total flying time (h)
D = density of birds
e = rate of passage (birds·km^{-1}·h^{-1})

Figure 7
Diagram illustrating the parameters discussed in section 3

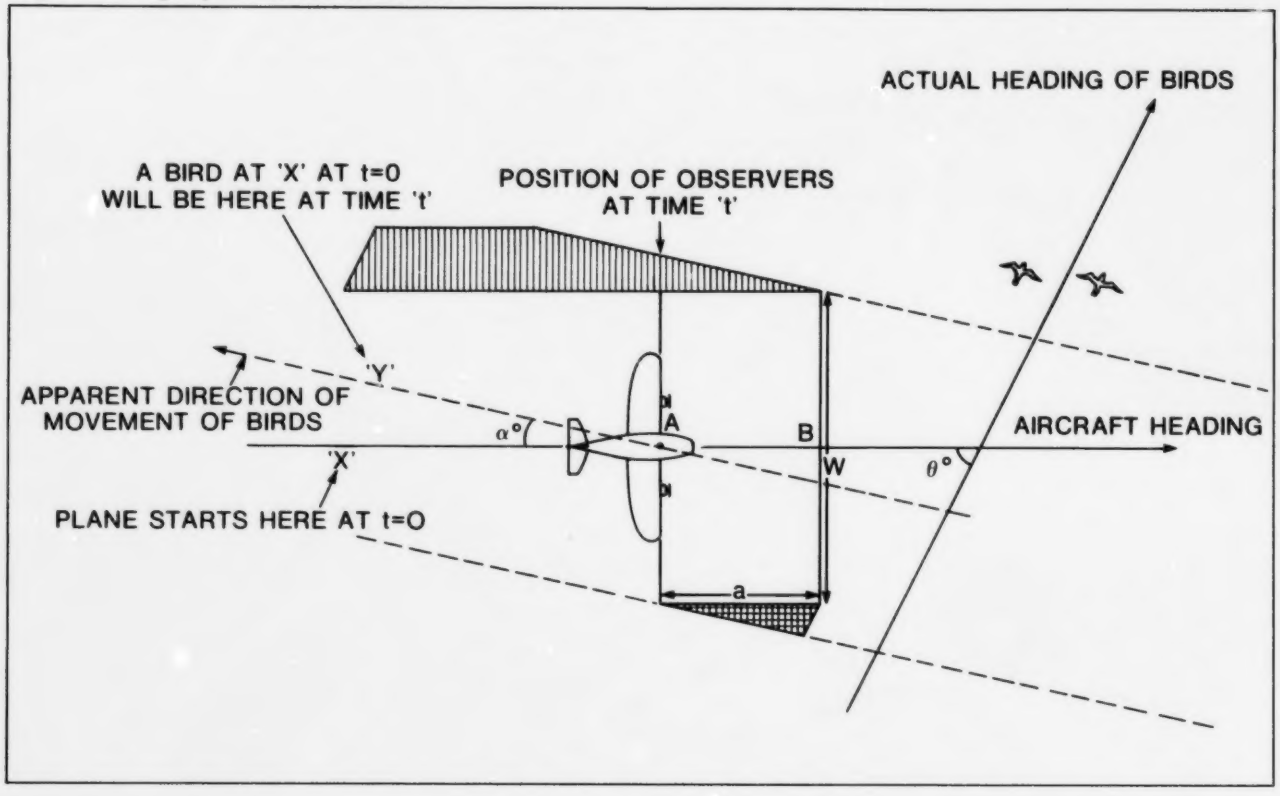
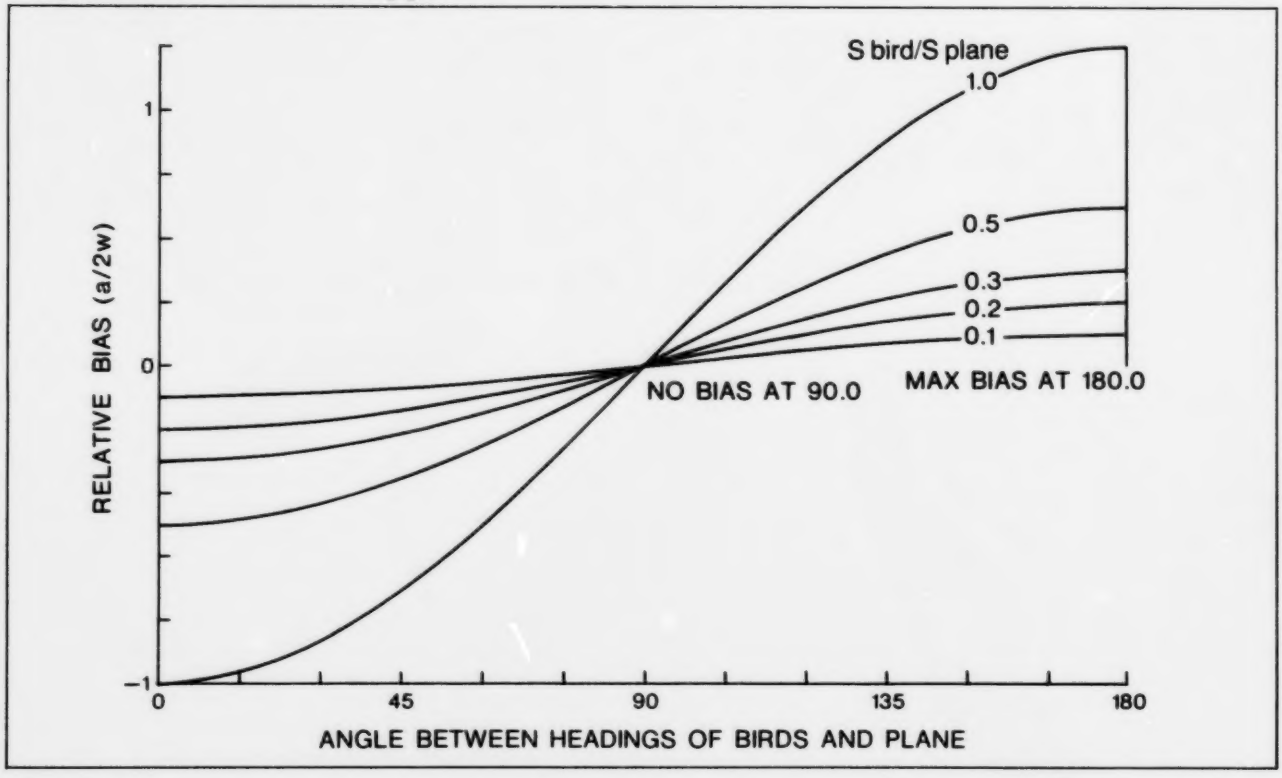


Figure 8
The relationship of observed to actual rates of passage (e_o / e_a) calculated from equations [4] and [5] for different speeds of birds and aircraft in relation to the angle θ°. Forward vision is assumed to be negligible



The relationship of e as calculated from formula [9] to e as calculated from formula [8] is plotted for different ratios of s to S and different values of θ in Figure 8, assuming that $a = 0$ (the observer does not look ahead of the plane). In this situation the correction is least important where $\theta = 45°$, and most important where $\theta = 135°$. Where forward vision is equal to the transect width, the correction required is greater, reaching a maximum at $\theta = 180°$, and a minimum at $\theta = 90°$ (Fig. 9). In all cases, the bias is greatest when the speed of birds and aircraft are the same, becoming fairly insignificant when the two speeds differ by a factor of 5 or more ($s/S < 0.2$). This correction is most likely to be of value when surveys are flown by helicopter, or when fast-flying species such as murres are recorded. As most species of seabirds fly at 40–60 km·h^{-1}, such a correction might also be usefully applied to shipboard observations where the speed of the ship exceeds 10 km·h^{-1}, using the generalized version of formula [9]:

$$e = \frac{Ns}{t(|S - s\cos\theta|W + as|\sin\theta|)} \qquad [10]$$

4. Duration and frequency of dives

The problem of errors introduced into aerial counts by seabirds diving at the approach of the aircraft is universally recognized. Species that normally dive below the surface for food pose an additional problem because, even without disturbance, a proportion of the birds present will be out of sight at a given instant.

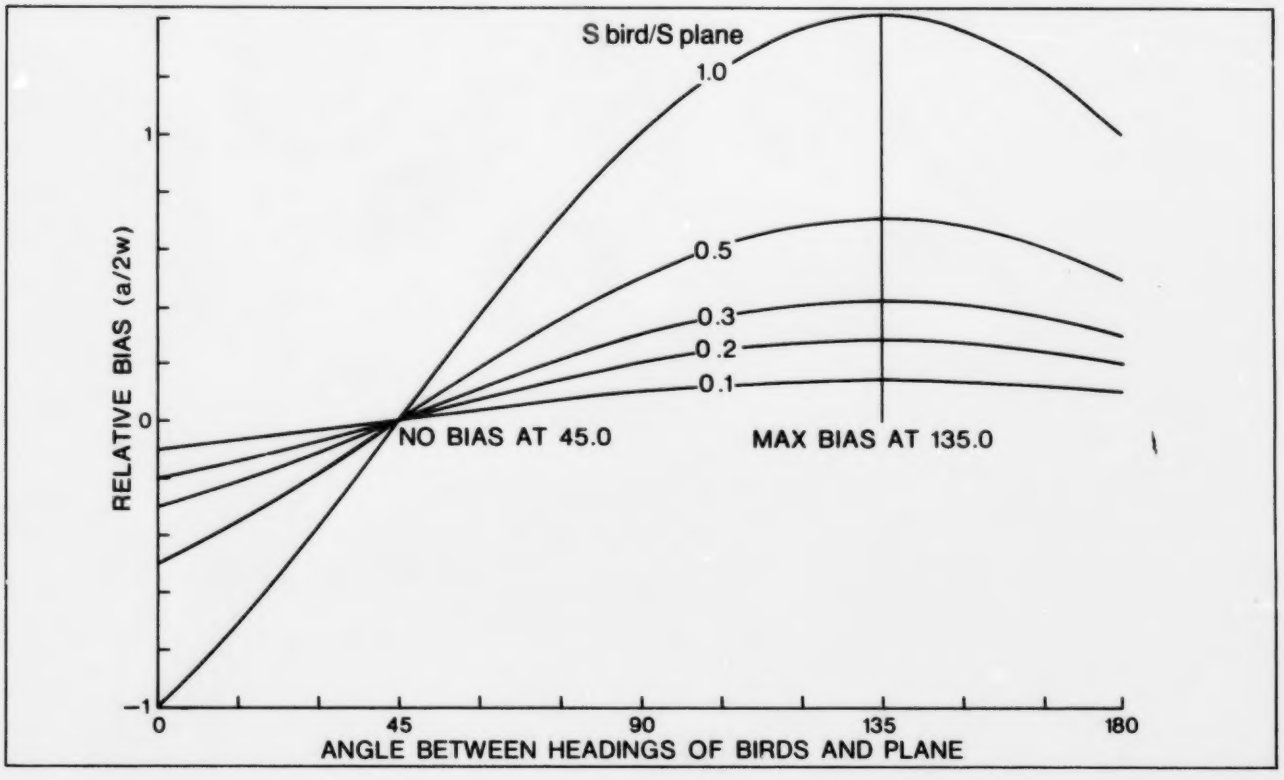
For most alcids, cormorants *Phalacrocorax* spp., and loons *Gavia* spp., the normal duration of dives is up to 2 minutes (Tuck 1961; Uspenski 1956; Cody 1973; Scott 1973; AJG, pers. obs.). The frequency of dives, however, is highly variable, and probably dependent on several imponderable factors. If the frequency and the duration of dives were constant for a given species, they would not affect comparisons of abundance between areas for individual species. Unfortunately, virtually nothing is known about variation in the frequency of dives, particularly for areas away from coastal waters.

Where some measure of the proportion of time spent under water is available, a correction for observed densities might be possible, using the formula:

$$N_f = N_o \Big/ \frac{s}{s + u} \qquad [11]$$

where u = mean duration of dives, and s = mean interval between dives. McLaren (1961), who worked on ringed seals, gives a more sophisticated formulation for this correction factor, which takes into account the number of submerged animals that surface during the time a given piece of water is under observation:

Figure 9
The relationship of observed to actual rates of passage (e_o / e_a) calculated for Figure 7, but assuming forward vision is equal to transect width



$$N_f = N_o \Big/ \left(\frac{s}{s+u} + \frac{t}{s+u} \right) \qquad [12]$$

where t = duration a given spot on the water is under observation (for derivation see Eberhardt 1978).

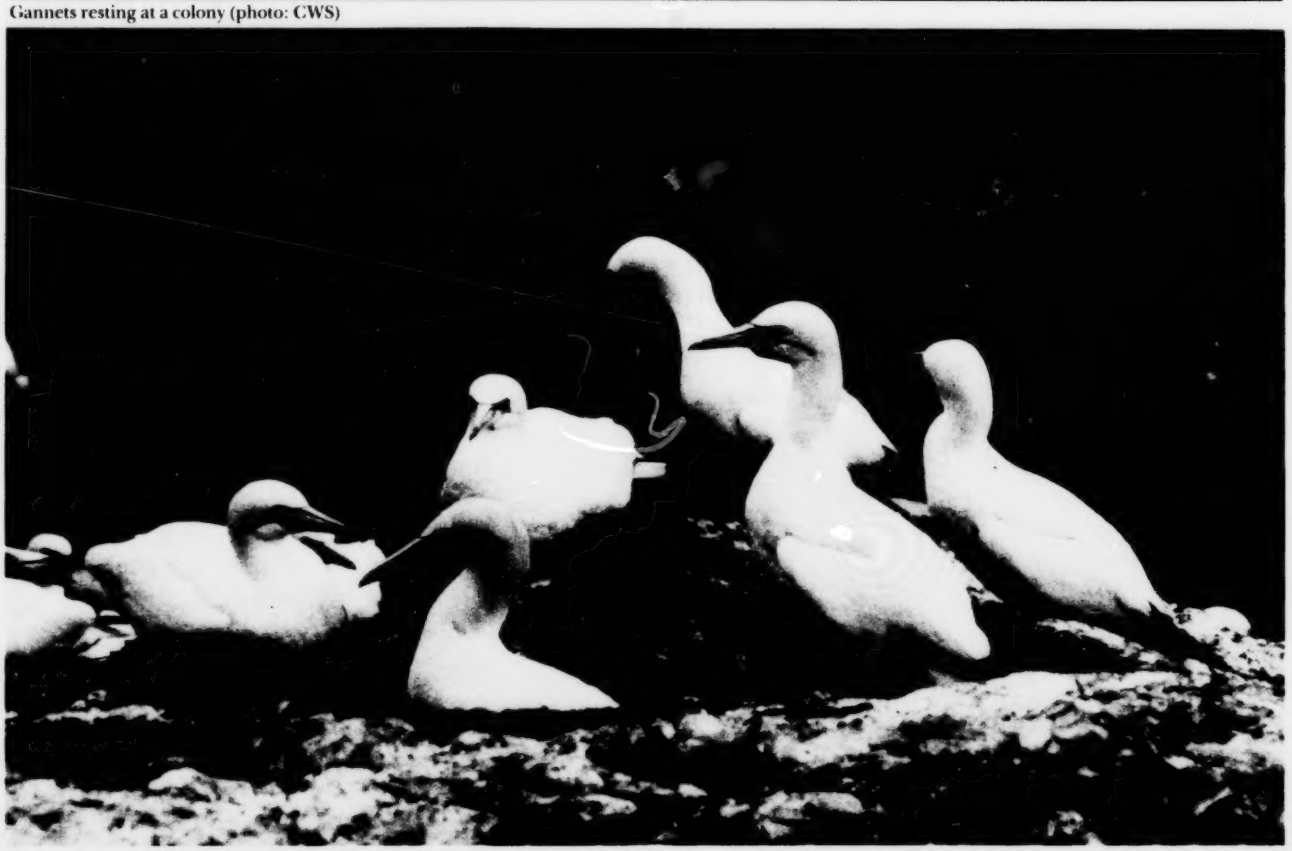
In aerial surveys, the length of time a given point on the water is in view is usually rather short (<10 s). As a result, the term $t/(s + u)$ assumes a negligible importance. Conversely, for most observations from boats, t is likely to be large relative to $s + u$ so that most submerged birds will surface during the time the observer scans a given area of water. Thus, the correction for submerged birds becomes unnecessary. Casual observations suggest that the ratio $(s + u)/s$ rarely approaches 2. It is unlikely that this correction could be very widely applied to aerial surveys because of the difficulty of determining the proportion of birds actually diving.

Most species of sea ducks (eiders *Somateria* spp., Oldsquaw *Clangula hyemalis*, scoters *Oidemia*, *Melanitta* spp.) tend to dive synchronously while feeding so that over a small area a very large variation in the number of birds recorded may occur, depending on whether a flock (sometimes several hundred birds) is either "up" or "down". This effect may help to explain some of the large discrepancies reported between ground and aerial surveys for sea ducks (Stott and Olson 1972, Savard 1982).

A related issue is the tendency of birds to flush or dive when they detect an aircraft. Usually, species that spend most of their time flying (gulls, petrels, etc.) take to the wing and hence become more conspicuous to the observer, while those that do little flying (auks, loons) tend to dive below the surface. Sometimes flying auks and, occasionally, some sea ducks will plunge directly into the sea at the appearance of an aircraft without alighting on the surface first. This behaviour is particularly common among Dovekies *Alle alle*.

Although these responses are clearly related to species-specific behaviour, they are probably much affected by other factors, such as the type of aircraft, the altitude at which it is flying, and the background noise caused by wind and waves. We cannot, therefore, recommend any suitable correction factor but can merely suggest that the problem be borne in mind when comparing surveys made in different types of aircraft or with different survey procedures.

Gannets resting at a colony (photo: CWS)



5. Degree of aggregation

Some seabirds normally occur in flocks, whose size may vary seasonally and among different geographic areas. In many cases, these flocks are very compact (Black-legged Kittiwakes, Dovekies, eiders), and thus the flocks, rather than the individuals, are the units recorded. Burnham *et al.* (1980) discussed the effects of these aggregations on transect results, but they did not explore the effects of aggregation on the relationship between survey intensity and accuracy.

The accuracy of survey results depends on the area included within the transect strips, relative to the total area involved (survey intensity). However, for a given area covered by transects the accuracy of the resulting estimates depends on the frequency with which recording units (individuals or flocks) are encountered. For a fixed population, the number and density of flocks is inversely related to their mean size. Hence, to obtain the same level of accuracy, survey intensity must increase with flock size. We illustrate this relationship for some hypothetical examples in Figure 10 (see Appendix 3).

Most transect sets used by aerial surveys cover a relatively small proportion of the whole area (<5%). Moreover, flock sizes for certain species may reach hundreds, occasionally thousands, of birds. Consequently, flocking may greatly constrain the accuracy of surveys for some species. Figure 11 may be used as a guide to the reliability of surveys in relation to flock size and the total population involved. The latter may be known approximately from estimates of local breeding birds. For flock sizes and populations above and to the left of the diagonal lines in Figure 10, surveys covering less than 5% of the total water area can be regarded as unreliable, as the coefficient for variation in resulting estimates will exceed 50%.

Nettleship and Gaston (1978) surveyed four species in Barrow Strait and Lancaster Sound, and their approximate position is also illustrated in Figure 11. Survey intensities, which varied from 1.5 to 3.5% of the total area, were probably adequate for Northern Fulmar, Thick-billed Murre, and Black Guillemot, but were less reliable for Black-legged Kittiwake. In their study, the authors themselves suggested this conclusion.

Figure 10
Survey intensity required to obtain a given coefficient of variation for a population estimate, in relation to flock size: A, coefficient of variation = 10%; B, coefficient of variation = 30%

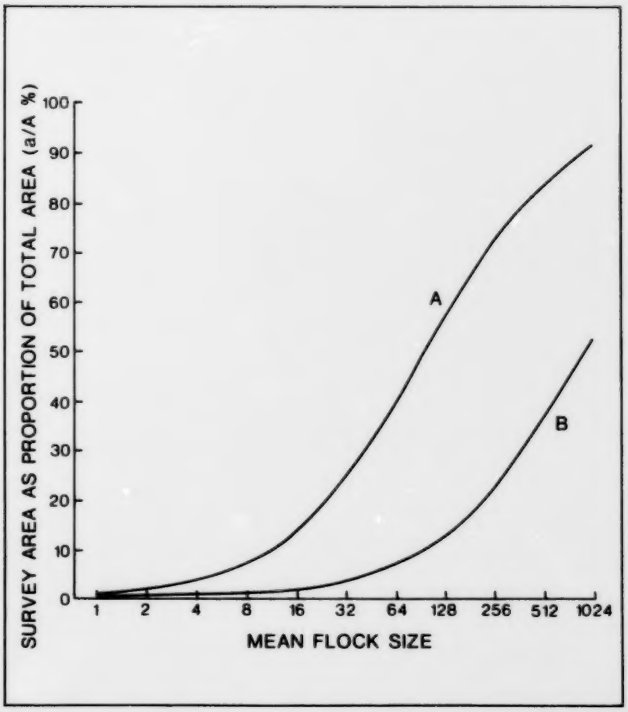
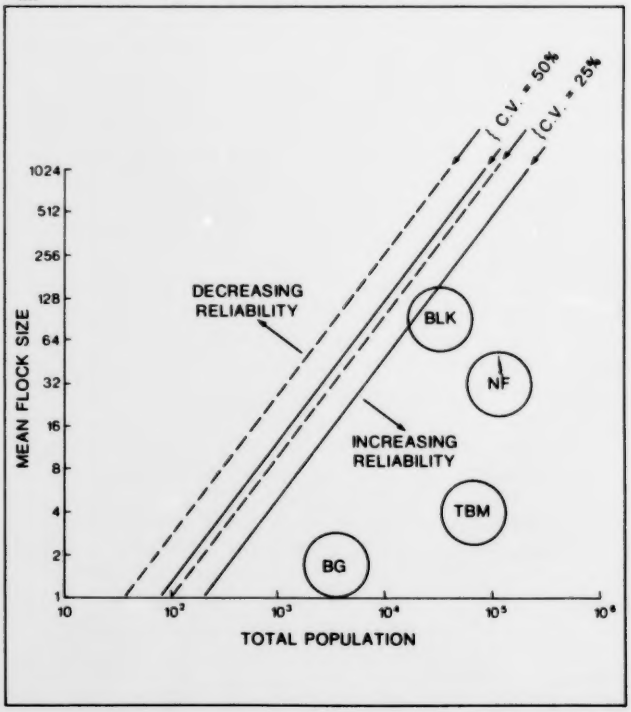


Figure 11
Guide to the reliability of estimates derived from aerial surveys in relation to the total population and the mean flock size; solid lines represent surveys where the transect strips incorporate 5% of the total area, broken lines 2%. Also shown are approximate population/flock size plots for species recorded by Nettleship and Gaston (1978); NF = Northern Fulmar, BLK = Black-legged Kittiwake, TBM = Thick-billed Murre, BG = Black Guillemot



Discussion

As several of the situations described refer to the analysis of surveys carried out during the breeding season, the corrections suggested require knowledge of the breeding biology of the species concerned. Ideally, when aerial surveys to record seabird distribution during the breeding season are contemplated, they should be combined with simultaneous observations at colonies of the major species involved. Compared with the cost of aerial surveys, colony observations will probably be fairly small; moreover, they will improve the information obtained from the surveys. The most pertinent data are the frequency of colony visits, as measured by rates of incubation exchange and chick-feeding, and the time spent on the colony by each member of a pair. Direct comparisons between numbers at the colony and counts of birds at sea may also be useful in validating the results of aerial surveys.

Where a correction for the relative speed of birds and aircraft is required, the angle between the headings of the two must be plotted. This method is difficult to apply in the field, however, because birds may alter course in response to the presence of the aircraft. If the birds involved are clearly flying to or from a major colony, it may be possible to get an adequate estimate of their headings by taking a bearing of the colony from the aircraft's position. Otherwise, the heading of distant birds, judged to be too far off to be influenced by the aircraft, must be used. The distance at which the observer can identify birds ahead of the aircraft must also be estimated and recorded. In any case, it may be useful to document this distance because it determines how long a bird is visible to the observer. This length of time, in turn, presumably affects the accuracy with which the observer can identify the bird or, in the case of a flock, estimate the number of birds present.

Another area where additional information could improve the interpretation of survey results is in quantifying the amount of time spent underwater by different diving species and the way in which this varies with time of day and time of year. This entails timing not only the dive and rest periods during bouts of feeding, but also the duration of feeding and resting bouts. It may also be possible to measure the responses of birds to aircraft at different distances and altitudes.

Although we have chosen to concentrate on biases and inaccuracies caused by the behaviour of the birds, it is obvious that these interact with other survey variables; weather, aircraft type, survey procedures, and observer differences. In the face of such a plethora of interacting and confounding variables, the whole idea of aerial surveys at sea becomes questionable. Fortunately, most surveys are carried out over a limited period, within which weather conditions and bird behaviour may be expected to be reasonably uniform. If, in addition, the same observers and aircraft are used repeatedly, a huge source of potential bias will be removed. However, when comparisons are made between small numbers of surveys, carried out with different aircraft, by different personnel, at different times of year, and under different survey procedures, the task of making quantitative judgements becomes impossible and we probably reach the limits of usefulness for this type of survey.

Appendices

Appendix 1

Method used to correct observed densities for differences in travel time

This method is used to derive correction factors for observed bird densities, where birds that are feeding and those commuting to and from feeding areas are not distinguished. Divide the area within the foraging range of the colony, but excluding the colony itself, into concentric zones 1, 2, 3, . . . , z (Fig. 4). Zone i includes the area from L_{i-1} to L_i km from the colony.

Let
- V = daily number of visits made to the colony by each bird
- S = flight speed
- L = distance from colony to point where bird is observed
- T_b = total time each bird spends on the colony per day
- n_{oi} = average number of birds feeding in, or flying over, zone i at a given moment
- n_{fi} = average number of birds feeding in zone i at a given moment
- N_{fi} = total number of birds using zone i for feeding
- m_{ij} = average number of birds feeding in zone j which are passing over zone i at a given moment
- $n_{oz} = n_{fz}$ = number of birds feeding in, or flying over, the outermost zone

For any zone i the number of birds feeding at a given moment is the total number present minus the number that are travelling to and from more distant zones, i.e.:

$$n_{fi} = n_{oi} - \sum_{j=i+1}^{z} m_{ij} \qquad [A1]$$

Now, of the N_{fj} birds using zone j to feed, the average number flying over zone i at a given moment is:

$$m_{ij} = 2VN_{fj}(L_i - L_{i-1})/24S \qquad [A2]$$

Also, a bird feeding L km away from the colony spends $24 - T_b - 2VL/S$ hours actually feeding, i.e. a fraction

$$1 - \frac{T_b}{24} - \frac{VL}{12S}$$

of the birds are actually feeding at any given time.

To visit zone i, birds must spend $(2L_{i-1})/S$ hours travelling. Hence:

$$N_{fi} = \frac{2n_{fi}}{24 - T_b - 2VL_{i-1}/S} \qquad [A3]$$

Substituting [A2] and [A1] into [A3], we obtain

$$N_{fi} = \frac{24n_{oi} - [2V(L_i - L_{i-1}) \sum_{j=i+1}^{z} N_{fj}]}{(24 - T_b)S - 2VL_{i-1}} \qquad [A4]$$

The N_{fj} can be calculated successively, beginning with the outermost zone, z, where:

$$N_{fz} = \frac{24n_{oz}}{24 - T_b - (2VL_{z-1})/S}$$

Appendix 2

Corrections for the relative motion of birds and aircraft

1. Derivation of formula for rates of movement based on aircraft observations

In this section we shall derive an expression to calculate the rate of movement (i.e. the number of birds per unit time crossing a line of unit length perpendicular to the birds' flight path) when the observations are made from a moving platform (i.e. plane, boat, etc.).

First, let us derive an expression that relates the density of birds, their speed, and their rate of movement. Consider a 1 km × 1 km area with birds entering at right angles to one side.

s = velocity of birds (km·h^{-1})
e = rate at which birds cross one side per unit length (h^{-1}·km^{-1})
D = density of birds (km^{-2})

Each bird spends s^{-1} h in block. Therefore, to maintain D birds in the block, D birds must enter every s^{-1} h.

$$\text{Therefore, } e = D/s^{-1} = Ds \qquad [A5]$$

As we know s, we will be able to find the rate of movement, e, if we can estimate D.

Let us consider the situation in Figure 7 where:
1) the birds' speed is s km·h^{-1}
2) the platform's speed is S km·h^{-1}
3) the birds are flying at an angle $\theta°$ to the platform
4) the transect width is w km
5) the birds are observed ahead on the transect for a distance of a km

To simplify the derivation we will assume $\theta > 0$, i.e. the birds fly in an upward direction in Figure 3 and the component of velocity of the birds in the direction the platform is proceeding, $s\cos\theta$, is less than the platform's speed S, i.e. the platform gains on the birds, or $S - s\cos\theta > 0$.

For every S km the platform moves to the right in Figure 3, the birds move $s\cos\theta$ km to the right, and $s\sin\theta$ km up. Hence, relative to the platform, every t hours the birds move $(S - s\cos\theta)t$ km to the left, and $st\sin\theta$ km up. Thus, from the platform the birds appear to be flying at an angle θ given by:

$$\tan\theta = \frac{s\sin\theta}{S - s\cos\theta} \qquad [A6]$$

The vertical hatching in Figure 7 represents the positions at time t of birds who were seen by the observers but are no longer in the field of view. Although observers count birds only within $w/2$ km of either side of the aircraft, giving a transect width of w, the effective width of the transect is greater than w because some birds will enter the field of view (cross-hatched area in Fig. 7) through the lower side of the rectangle rather than from the front.

The extra width given to the transect by the fact that the observers count birds up to a units ahead is:

$$w_a = a\tan\theta = \frac{as\sin\theta}{S - s\cos\theta}$$

Therefore, transect width is actually:

$$W = w + w_a = w + \frac{as\sin\theta}{S - s\cos\theta}$$

Hence, in t hours, the area viewed by the observers is:

$$A = W(S - s\cos\theta)t + aw$$

If N birds are counted in t hours, the bird density is $D = N/A$, and from equation [1], the number of birds crossing a 1-km line per hour is:

$$e = Ds = \frac{Ns}{A} = \frac{Nv}{t\left[\frac{w + as\sin\theta}{S - s\cos\theta}\right](S - s\cos\theta) + aw} \qquad [A7]$$

$$e = \frac{Ns}{t((S - s\cos\theta)w + as\sin\theta) + aw}$$

If the cross-hatched area were omitted, as would be the case if the transect were flown, and the data recorded in segments of equal time or length (as this portion would have been counted on the previous segment), then:

$$e = \frac{Ns}{t((S - s\cos\theta)w + as\sin\theta)} \qquad [A8]$$

This correction was derived under the assumption that $S - s\cos\theta > 0$ and $\theta > 0$. If $S - s\cos\theta < 0$ (i.e. the birds "gain" on the observation platform, which might be the case if the platform were a boat rather than a plane), then the above argument would produce equation [3] but with $S - s\cos\theta$ replaced by $s\cos\theta - S$. Similarly, if $\theta < 0$ (i.e. the birds flew in a downward direction in Fig. 7), $\sin\theta$ would be replaced by $\sin(-\theta)$. In view of this, a formula applicable for all angles and platform speeds is:

$$e = \frac{Ns}{t(|S - s\cos\theta|w + as\sin|\theta|)} \qquad [A9]$$

We give some particular examples below:

1) If $\theta = 90°$; $\quad e = \dfrac{Ns}{tSw + as}$

2) If $a = 0$; $\quad e = \dfrac{Ns}{tw\,|S - s\cos\theta|}$

3) If $\theta = 90°$ and $a = 0$; $e = \dfrac{Ns}{tSw}$

2. Risk of not correcting for the motion of flying birds in aerial surveys

Let us now consider the bias introduced if we do not correct for the speed and direction of the flying birds. One might argue that we can omit the effect of their movement because the platform (in this case the airplane) travels much faster than the birds. If we do, then the estimate of density, D, as defined before equation [1] is D = (number of birds seen)/(total area scanned from platform), or $D = N/(tSw)$. Hence, from [1], the uncorrected migration rate is:

$$e_1 = Ns/(tSw) \qquad [A10]$$

From [4] and [5], the relative bias in e_1 is:

$$B = (e - e_1)/e$$
$$= 1 - \left(\left| 1 - \frac{s}{S} \cos\theta \right| + \frac{a}{w} \cdot \frac{v}{S} |\sin\theta| \right) \qquad [A11]$$

Thus, B depends only on the ratio of the birds' speed (s) to the platform's speed (S), on the ratio of the sight distance ahead (a) to the transect width (w), and on the angle θ.

As it makes no difference to the calculations whether the birds enter the plane's flight path from the right or the left, we will assume θ is between 0° and 180°, i.e. they enter from the right. Further, because we are considering aerial surveys, where the birds will fly slower than the platform, we assume $s/S < 1$. Hence, the above equation for bias becomes:

$$B = 1 - (R\cos\theta + KR\sin\theta) \qquad [A12]$$

where $K = a/w$ = sight distance/transect width, and $R = s/S$ = birds' speed/platform's speed.

Figures 8 and 9 show the biases inherent in equation [A9] for various values of K, R, and θ. We note that, for θ near zero (birds fly in approximately the same direction as the platform), B is negative, i.e. the rate, e, is underestimated. For large θ (birds fly in the opposite direction), B is positive and e is overestimated. Further, the bias becomes more serious the larger R becomes. If we compare the figures, we see that the bias is more serious the larger K is, i.e. we count birds on the transect a long distance ahead.

For particular values of R and K, equation [A12] together with Figures 8 and 9 show that the bias has a maximum negative value of $B_0 = -R$ when $\theta = 0°$, that it increases to zero as θ increases to $\theta = \arctan(1/K)$, continues to increase to a maximum of $B_{max} = R\sqrt{1 + K^2}$ as θ increases to $\theta = \arctan(-K)$, and then decreases to $B_{180} = R$ for $\theta = 180°$.

Let us now calculate B for some specific cases. Suppose $R = 0.3$ and $K = 0.5$, i.e. the birds are flying at 30% of the speed of the aircraft and the observers do not count ahead of the aircraft. Then, from the previous paragraph, B will range from –0.3 when $\theta = 0°$ to +0.3 when $\theta = 180°$ (Fig. 8, $B = 0.3$). If $K = 1.0$, i.e. the observers see as far ahead as the width of the transect, then B ranges from –0.3 when $\theta = 0°$ to a maximum of +0.43 when $\theta = 135°$ (Fig. 9). These biases are systematic errors unaffected by sample size.

In estimating the density or the rate of movement, it is an advantage to include birds on the transect that are well ahead of the plane. This approach tends to increase the number of birds counted and hence the ultimate accuracy of the estimate provided:

(1) the observers can accurately determine whether a bird on the transect is within the given sight distance (a).

(2) the birds are clearly visible at a distance "a" ahead of the plane.

(3) the motion of the birds is taken into account when estimating rate of movement (e) or density (D).

Appendix 3

Derivation of the relationships among flock size, total population size, and the level of accuracy obtained for a given proportion of the area surveyed

Let A = total area of interest
a = total area covered by transect strips
N = number of birds in area A
M = number of flocks in area A
n = mean flock size

We assume:
(1) n is constant (hence, $n = N/M$)
(2) flocks are randomly distributed within the area

Then the number of flocks counted (y) has a binomial distribution with mean $E(y) = Mp$ and variance $Mp(1 - p)$, where $p = a/A$.

Hence, N can be estimated by:

$\hat{N} = ny/p$ with variance estimated by
$V = nN(1 - p)/p$

$$\text{Thus: } \frac{a}{A} = \frac{Nn}{V + Nn} \qquad [A13]$$

Using this equation we examine the relationship between flock size, n, and the survey intensity, a/A, required to estimate a population of a given size, N, with a given variance, V (Fig. 10). Alternatively, we can examine the relationship between flock size and total population when the variance and the survey intensity are fixed (Fig. 11).

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